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The male terminalia of seven American species of *Drosophila* (Diptera, Drosophilidae)

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Abstract

The male terminalia of seven species of *Drosophila* endemic to the New World are described or redescribed and illustrated: one in the *hydei* subgroup (*D. guayllabambae*) and four in the *mulleri* subgroup (*D. arizonae*, *D. navojoa*, *D. nigrodumosa*, and *D. sonorae*) of the *repleta* group; one in the *sticta* group (*D. sticta*) and one so far unassigned to group (*D. comosa*). The *D. guayllabambae* terminalia redescription is based on a wild-caught fly. The redescriptions of the terminalia of the four species in the *mulleri* subgroup are based on strain specimens, while those of *D. sticta* and *D. comosa* terminalia are based on their holotypes. *D. guayllabambae* seems to be a strictly mountainous species of the Ecuadorian and Peruvian Andes. *D. nigrodumosa* is apparently endemic to Venezuela, occurring in the Andes as well as at lower altitudes. The remaining five occurs only at lower altitudes of the American continent. The detailed line drawings depicted in this paper aim to help interested taxonomists to tell those species apart. Their precise identification is of great importance to the knowledge of the American biodiversity increasingly threatened by human activities.

Introduction

Since early last century, the male terminalia have been the main feature used by entomologists to identify sibling species of insects, including flies of the genus *Drosophila*. Having this in mind, during the past forty years I have dedicated myself to clarify the identity of dozens of species of *Drosophila* mostly endemic to the American continents. Several line drawings of male terminalia prepared during this period have already been published (e.g. Vilela and Sene 1977, Vilela 1983, Vilela and Bächli 1990, Vilela et al. 2008). These were meant, in part, to complement those previously published by other authors (e.g. Duda, 1927, Wasserman 1962). Drawings of some species treated in the present paper were already published in the last 30 years by different authors (Rafael and Arcos 1988, Fontdevila et al. 1990, Ruiz et al. 1990, Heed and Castrezana 2008), although depictions of male sclerites in different views were offered.

In addition to specimens deposited in the *Drosophila* type and reference collection (DTRC) curated by Dr. Marshall R. Wheeler, all species strains belonging to the *Drosophila repleta* group formerly maintained at the University of Texas at Austin were examined in 1979. At that time, the author described the male terminalia of four undescribed species in his PhD thesis (Vilela 1981). However, for different reasons, they were not included in the resulting article entitled "A revision of the *Drosophila repleta* species group (Diptera, Drosophilidae)" by Vilela (1983). These four species are as follows: *D. arizonae* Ruiz, Heed & Wasserman, 1990, *D. navojoa* Ruiz, Heed & Wasserman, 1990, *D. nigrodumosa* Wasserman & Fontdevila in Fontdevila et al., 1990, and *D. sonorae* Heed & Castrezana, 2008.

Yet in 1979, the author also examined the spot-thoraxed female holotype of *Drosophila peruensis* Wheeler, 1959 in the DTRC, collected in 1903 somewhere along the Urubamba River, Peru. Based on the wing pattern

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and the morphology of the arista, the author proposed to transfer it from the *repleta* species group to the *guarani* species group (Vilela 1983). In late February 1984, the author searched for a male specimen of *Drosophila peruensis* making a visit to the Urubamba Canyon at the end of the railroad track (Fig. 1) running from Cuzco to Machu Picchu (km 112). This final station is located just above the bridge crossing the Urubamba River (Reparaz 1984: 197, 201) at the beginning of the unpaved zigzag road (Hiram Bingham) going up to the Machu Picchu ruins (ca. 2400 m altitude; Fig. 2A). One banana-baker's yeast-baited trap was placed on the rocks at 1 km northeast of the Machu Picchu station (13°09'S; 72°32'W) alongside the railroad (km 111, Fig. 2B). On March 2nd seventeen specimens (6 males, 11 females) of an undescribed species were collected and later misidentified and redescribed (Vilela and Pereira 1985, Vilela and Bächli 1990: 78) as *D. peruensis*. Nine years later, the previously misidentified and redescribed Peruvian specimens were renamed by Vilela and Pereira (1993) as *Drosophila urubamba*, included in the *guarani* group, and *D. peruensis* was transferred to a new group of its own (Ratcov and Vilela 2007). Additionally, one *Drosophila* male belonging to an undescribed species of the *hydei* subgroup of the *repleta* group was collected in the same trap and date. The specimen was dissected and its terminalia illustrated. This latter species would be formally described four years later (Rafael and Arcos 1988) as *Drosophila guayllabambae* based on specimens sampled from an isofemale line established from a single gravid female collected at 2200 m altitude in Ecuador.

In December 1985 and February 1989, aiming to clarify the identity of some poorly known American *Drosophila* other than those belonging to the *repleta* group, the author received two type specimens from the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., USA. These included a male holotype of *Drosophila sticta* Wheeler, 1957 (from Honduras), belonging to the *sticta* group, and a male holotype of *Drosophila comosa* Wheeler, 1968 (from Costa Rica), an ungrouped species. These were dissected and their terminalia described or redescribed and illustrated but never published.

The purpose of this paper is to clarify the identities of seven of the American *Drosophila* species cited above, five of them (members of *repleta* group) apparently associated with rotting cacti.

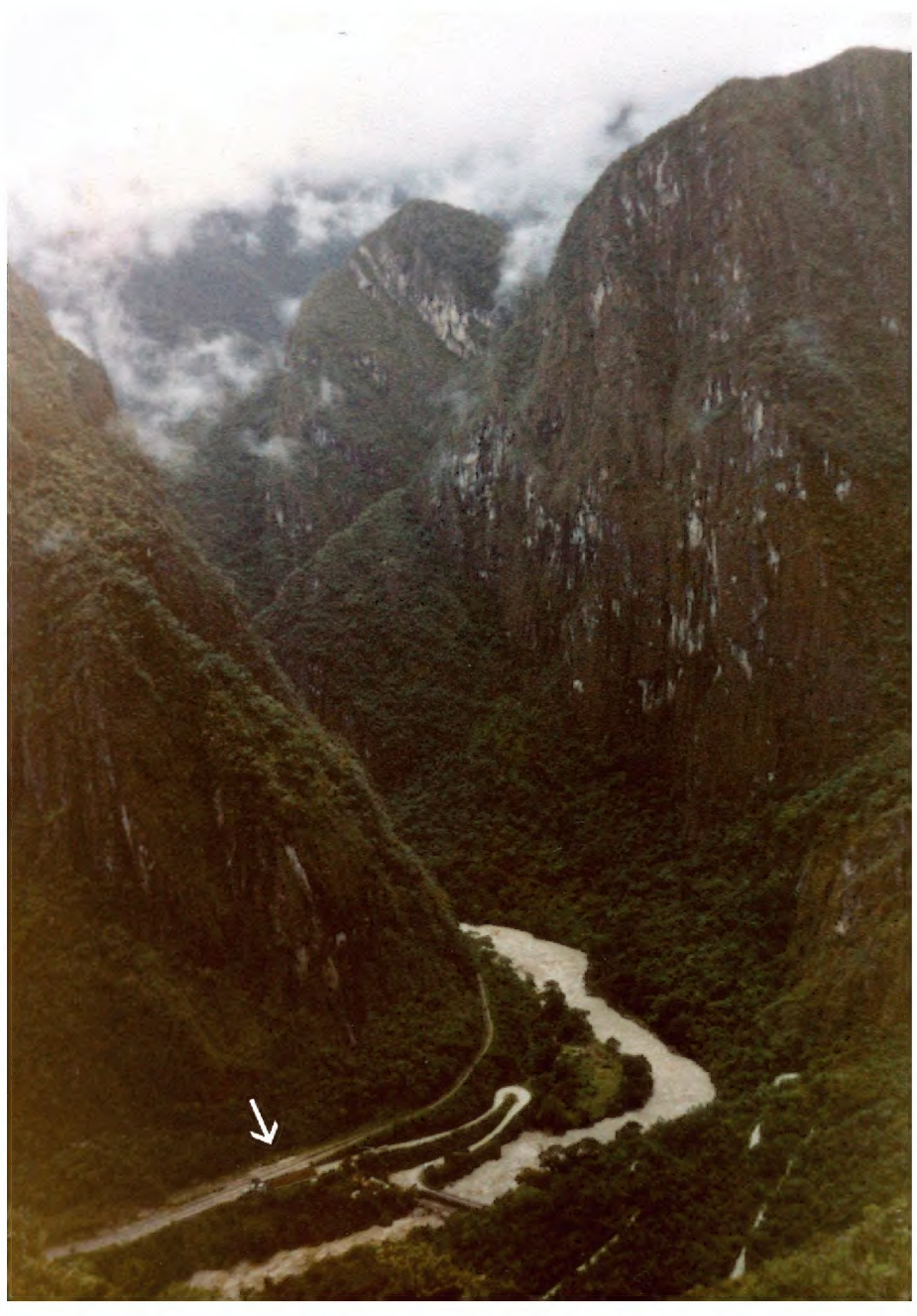

Figure 1. Urubamba Canyon (as seen from Machu Picchu ruins), Department of Cuzco, Peru. III.1984, C.R. Vilela phot. Arrow points the final stop of the railroad at km 112 marker (Estación Ferrocarril de Machu Picchu, that no longer exists).

Figure 2. Collection sites C49 (13°09'S, 72°32'W) and C50 (13°09'S, 72°32'W): Urubamba Canyon, Department of Cuzco, Peru. **A,** (C49) 1 km S of the final stop of the railroad, 01.III.1984, C.R. Vilela phot. **B,** (C50) 1 km NE (at km 111) of the final stop of the railroad, 02.III.1984, C.R. Vilela phot.

Material and methods

Male specimens belonging to seven American species of *Drosophila* were analyzed and had their terminalia illustrated. The dissected specimens, in alphabetical order, are as follows.

Drosophila arizonae, two males from strain E2.2 (Navojoa, Sonora, Mexico); *D. comosa*, male holotype (Golfito, Costa Rica); *D. guayllabambae*, one male double mounted (1 km NE of Machu Picchu railroad station); *D. navojoa*, two males from strain E2.1 (Navojoa, Sonora, Mexico); *D. nigrodumosa*, two males from strain 514.8 (Mérida, Venezuela); *D. sonorae*, two males from strain E37.5c (Alamos, Sonora, Mexico); *D. sticta*, male holotype (Lancetilla, Honduras).

The nine non-type specimens were either collected by the author in Peru (the fourth one) or obtained in 1979 from stocks maintained in the National *Drosophila* Species Resource Center (NDSRC), originally at the Department of Zoology, University of Texas (Austin). The NDSRC is currently named *Drosophila* Species Stock Center of the University of California at San Diego, which is on the way to be moved to Cornell University in New York.

The following non-dissected specimens were also sampled simultaneously from the same stocks: *D. arizonae* (22 ♂♂, 36 ♀♀), *D. navojoa* (23 ♂♂, 14 ♀♀), *D. nigrodumosa* (3 ♀♀), and *D. sonorae* (8 ♀♀).

All double-mounted non-type specimens cited above are deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil (MZSP).

Additionally, four double-mounted specimens (1♂, 3♀♀) sampled from each of the three Mexican stocks and from the Venezuelan strain maintained in the NDSRC were originally deposited in the DTRC (at the University of Texas, Austin) and later transferred to the AMNH (American Museum of Natural History, New York).

The analyzed and dissected type material includes the male holotypes of the poorly known *Drosophila comosa* and *Drosophila sticta*, both housed in the collections of the National Museum of Natural History, Washington, D.C., USA (NMNH).

Dissections of terminalia were performed following Wheeler and Kambysellis (1966), as modified by Kaneshiro (1969). For morphological terminology, measurements, indices, preparations of microscope slides as well as illustrations refer to Vilela and Bächli (1990, 2000) and Bächli et al. (2004). All line drawings in the same plate were drawn to the same scale.

Results

repleta group
hydei subgroup

Drosophila (*Drosophila*) *guayllabambae* Rafael & Arcos

Fig. 3A–H

Drosophila (*Drosophila*) *guayllabambae* Rafael & Arcos, 1988: 167.

Non-type material. Wild-caught male coded C50, labelled "PERU Cuzco, 1 km NE E.F. [Estación Ferrocarril] Machu Picchu, 13°07'S, 72°32'W, C.R. Vilela coll., 02.III.1984 / *Drosophila guayllabambae* C.R. Vilela det."

Male terminalia. Epandrium (Fig. 3A) posteriorly microtrichose, except lobe; bearing ca. 4 upper, 2 median and 12 lower setae; ventral lobe triangle-shaped, partially covering surstylus. Cercus mostly microtrichose, anteromedially fused to epandrium (Fig. 3A, B). Surstylus not microtrichose, with about 13 cone-shaped prensisetae, 6 outer setae and 8 inner setae. Decasternum as in Fig. 3B. Hypandrium (Fig. 3C) shorter than epandrium, anterior margin convex; posterior hypandrial process and dorsal arch absent; gonopod not microtrichose, linked to paraphysis by membranous tissue, bearing one seta on anterior inner margin. Aedeagus (Fig. 3D–H) with a pair of pointed, ventral, long spurs on subdistal margins, slightly bifid dorsally at tip (in dorsal and ventral views, Fig. 3D, H), blunt and slightly expanded distally (in lateral view, Fig. 3F); dorsal cleft ca. 2/3 length of aedeagus (Fig. 3E); paraphysis not microtrichose, anteriorly narrow, distally wide and double-walled, linked to gonopod by membranous tissue, subdistally with 1–3 setulae at dorsal margin (Fig. 3D, E, G, H). Aedeagal apodeme about half aedeagus length and fused to it, curved ventrad, laterally flattened, posterodorsally bifid (Fig. 3E). Ventral rod slightly shorter than paraphysis, dorsoventrally flattened, completely fused to aedeagal apodeme.

mulleri subgroup

Drosophila (*Drosophila*) *nigrodumosa* Wasserman & Fontdevila

Fig. 4A–D

Drosophila (*Drosophila*) *nigrodumosa* Wasserman & Fontdevila in Fontdevila et al., 1990: 446.

Species "from Venezuela": Wasserman 1982a: 95; Wasserman 1982b: 54, 59.

Non-type material. strain 514.8 (25 km S of Mérida, Mérida, Venezuela) [nickname: bushy tail], 1979: 2 ♂♂ (dissected) plus 3 ♀♀ (MZSP); 1 ♂, 3 ♀♀ (AMNH).

Male terminalia. Epandrium (Fig. 4A) posteriorly microtrichose, bearing about 1 upper and 11 lower setae; ventral lobe remarkably concave on ventral margin, distally pointed sharply, partially covering surstylus. Cercus (Fig. 4A) mostly microtrichose, anteromedially fused to epandrium. Surstylus not microtrichose, with about 9 cone-shaped prensisetae in apical row, ca. 20 conspicuous outer cone-shaped setae, 2 outer and 4 inner setae of usual shape. Decasternum as in Fig. 4A. Hypandrium (Fig. 4A) about 1 ½ longer than epandrium, anterior margin convex; posterior hypandrial process and dorsal arch absent; gonopod not microtrichose, connected to paraphysis by membranous tissue, bearing one long seta on anterior inner margin. Aedeagus long (Fig. 4B–D), subdistally ex-

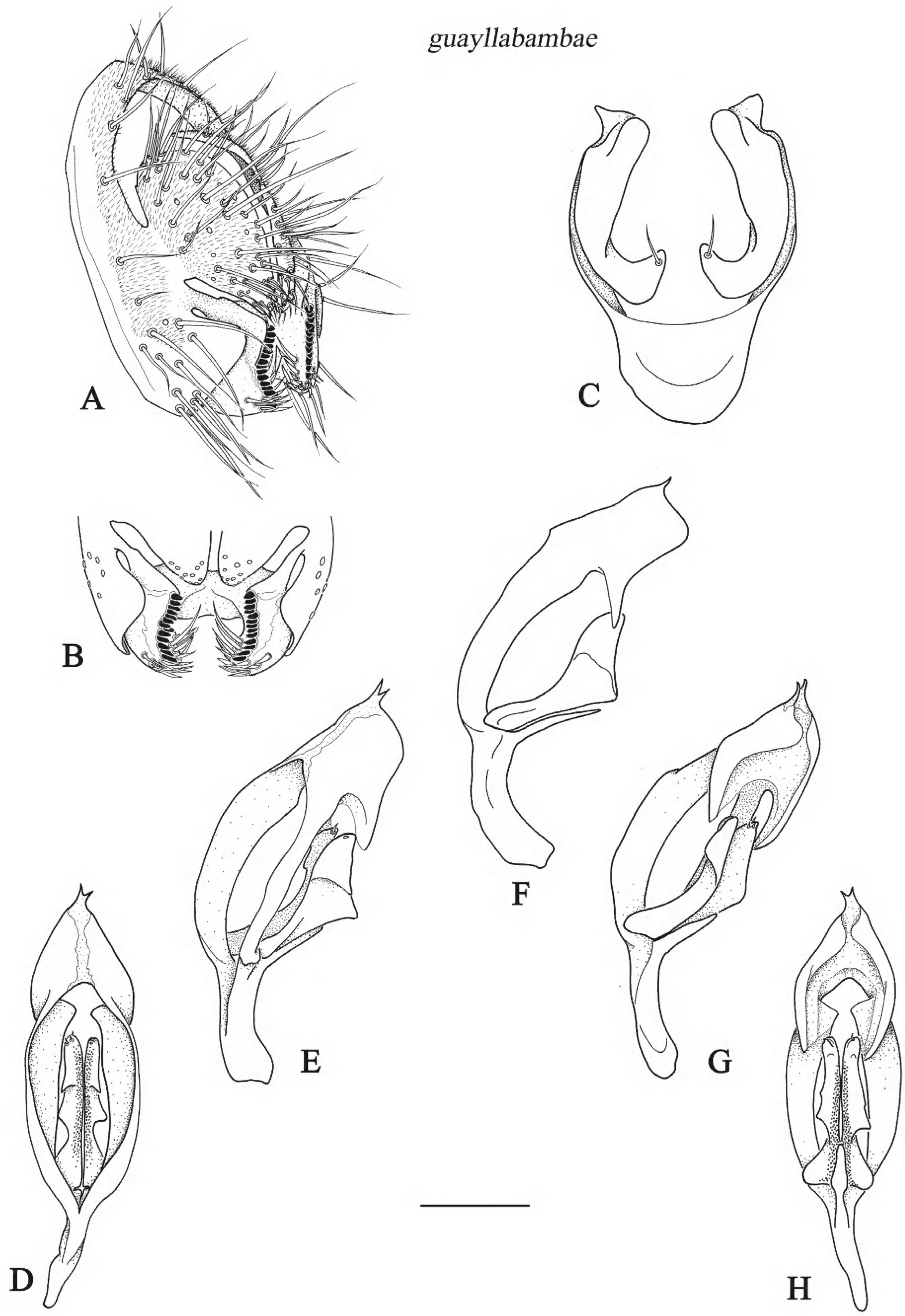

Figure 3. *Drosophila guayllabambae* Rafael & Arcos, 1988 (*repleta* group, *hydei* subgroup). 1 km NE of Estación Ferrocarril de Machu Picchu, Cuzco, Peru, 02.III.1984, C.R. Vilela coll., male terminalia (MZSP). **A,** epandrium, cerci and surstyli, oblique posterior view. **B,** surstyli and decasternum, posterior view. **C,** hypandrium and gonopods, posterior view. **D–H,** aedeagus, paraphyses and aedeagal apodeme, several views from dorsal through ventral. Scale bar: 0.1 mm.

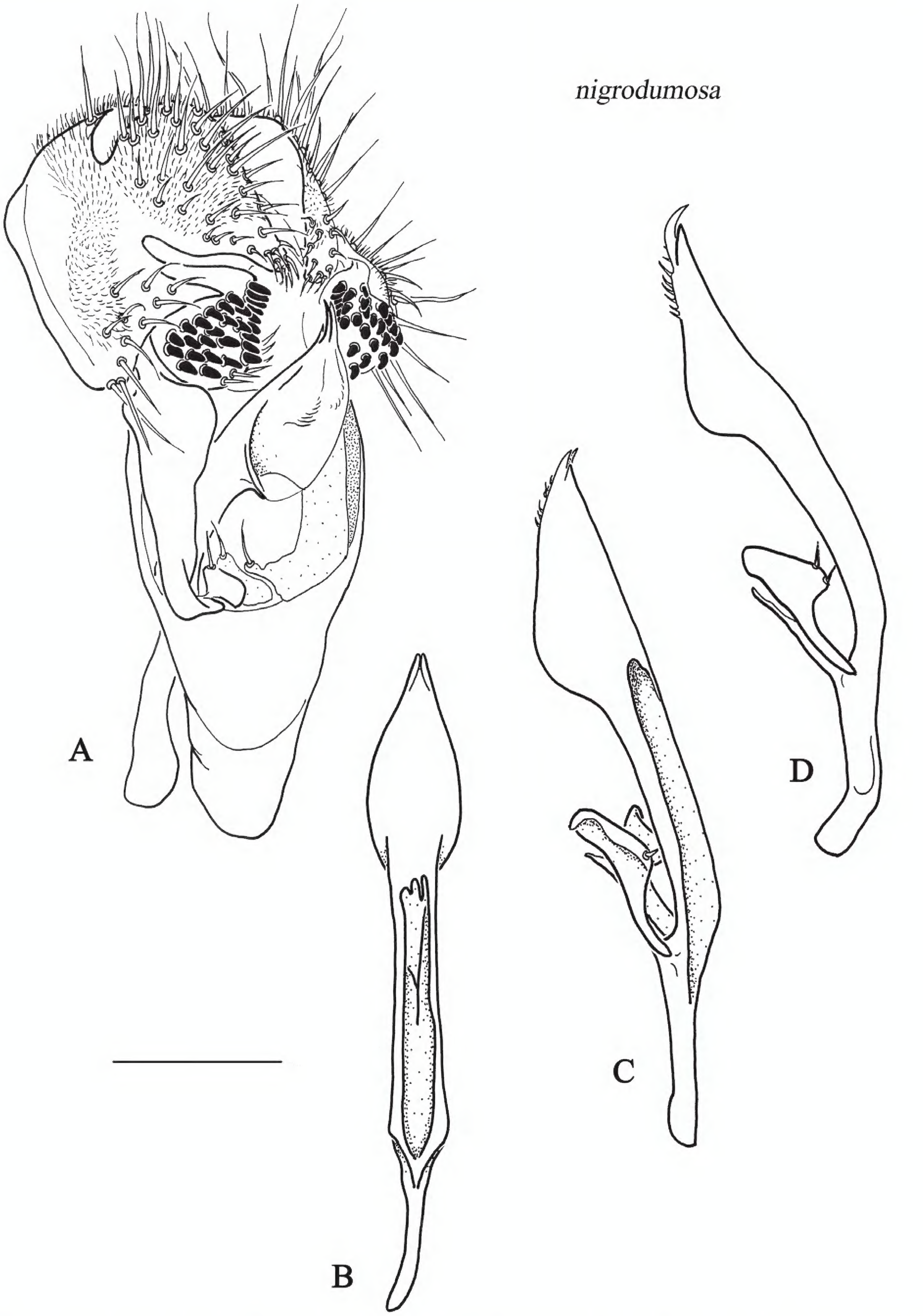

Figure 4. *Drosophila nigrodumosa* Wasserman & Fontdevila in Fontdevila et al., 1990 (*repleta* group, *mulleri* subgroup, *mulleri* complex). Strain 514.8 at NDSRC (type strain), from Mérida, Venezuela, male terminalia (MZSP). **A,** epandrium, cerci, surstyli, hypandrium, gonopods, aedeagus, paraphyses and aedeagal apodeme, oblique posterior view. **B–D,** aedeagus, paraphyses and aedeagal apodeme, three views. **B,** dorsal. **C,** oblique dorsal. **D,** right lateral. Scale bar: 0.1 mm.

panded dorsoventrally, bifid and slightly turned dorsad at dorsal tip (Fig. 4D); subapically microtrichose at ventral margin; dorsal cleft ca. 2/3 length of aedeagus (Fig. 4C); paraphysis not microtrichose, connected to gonopod by membranous tissue, narrow anteriorly, wide distally, submedially bearing 1–2 setulae dorsally. Aedeagal apodeme curved ventrad, laterally flattened, ca. 1/3 aedeagus length and fused to it, posterodorsally bifid (Fig. 4C). Ventral rod dorsoventrally flattened, completely fused to aedeagal apodeme.

Drosophila (*Drosophila*) *arizonae* Ruiz, Heed & Wasserman

Figs 5A–D

Drosophila (*Drosophila*) *arizonae* Ruiz, Heed & Wasserman, 1990: 39.

Non-type material. Strain E2.2 (Navojoa, Sonora, Mexico), 1979: 2 ♂♂ (dissected) plus 22 ♂♂, 36 ♀♀ (MZSP); 1 ♂, 3 ♀♀ (AMNH).

Male terminalia. Epandrium (Fig. 5A) distally microtrichose, except lobe; bearing about 8 upper and 9 lower setae; ventral lobe partially covering surstylus; ventral margin concave; anterior and distal end sharply pointed. Cercus mostly microtrichose; anteromedially fused to epandrium. Surstylus not microtrichose, with about 12–13 cone-shaped prensisetae, 2 outer and 11 inner setae. Decasternum as in Fig. 5A. Hypandrium (Fig. 5A) shorter than epandrium, anterior margin convex; posterior hypandrial process and dorsal arch absent; gonopod not microtrichose, connected to paraphysis by membranous tissue, bearing one seta on anterior inner margin. Aedeagus (Fig. 5B–D) short, weakly sclerotized at tip, submedially bearing a single ventral, anterad pointed spur (probably by fusion of two); dorsal cleft ca. 1/3 length of aedeagus (Fig. 5B); paraphysis not microtrichose, connected to gonopod by membranous tissue, distally double-walled, submedially bearing 1 setula adjacent to dorsal margin (Fig. 5C). Aedeagal apodeme curved ventrad, slightly shorter than aedeagus and fused to it, laterally flattened, posterodorsally bifid (Fig. 5B). Ventral rod as long as paraphysis, dorsoventrally flattened, completely fused to aedeagal apodeme (Figs. 5B–D).

Drosophila (*Drosophila*) *navojoa* Ruiz, Heed & Wasserman

Fig. 6A–D

Drosophila (*Drosophila*) *navojoa* Ruiz, Heed & Wasserman, 1990: 40.
Species "from Navojoa": Wasserman 1982a: 95–98; 1982b: 54, 57, 59.

Non-type material. strain E2.1 (Navojoa, Sonora, Mexico), 1979: 2 ♂♂ (dissected) plus 23 ♂♂, 14 ♀♀ (MZSP); 1 ♂, 3 ♀♀ (AMNH).

Male terminalia. Epandrium (Fig. 6A) dorsally microtrichose, slightly microtrichose on posterior medioventral area, with about 2 upper and 9 lower setae; ventral lobe narrow, distally round, not covering surstylus. Cercus mostly microtrichose, anteromedially fused to epandrium. Surstylus not microtrichose, with about 11–12 cone-shaped prensisetae, 1 outer and 3 inner setae. Decasternum as in Fig. 6A. Hypandrium (Fig. 6A) slightly shorter than epandrium, anterior margin convex; posterior hypandrial process and dorsal arch absent; gonopod not microtrichose, linked to paraphysis by membranous tissue, bearing one seta on anterior inner margin. Aedeagus (Fig. 6A–D) distally expanded dorsoventrally and bearing a bulbous, membranous, and microtrichose area; submedially bearing a single ventral, anterad pointed spur (probably by fusion of two); dorsal cleft ca. 4/5 length of aedeagus (Fig. 6B, C); paraphysis triangle-shaped, not microtrichose, connected to gonopod by membranous tissue, submedially bearing one setula on dorsal margin (Fig. 6D). Aedeagal apodeme shorter than aedeagus and fused to it, laterally flattened, dorsodistally bifid (Fig. 6B, C). Ventral rod as long as paraphysis, dorsoventrally flattened, completely fused to aedeagal apodeme (Fig. 6D).

Drosophila (*Drosophila*) *sonorae* Heed & Castrezana

Fig. 7A–D

Drosophila (*Drosophila*) *sonorae* Heed & Castrezana, 2008: 28.
Species "from Sonora": Wasserman 1982a: 95; 1982b: 54, 60; 1992: 508, 509.

Non-type material. Strain E37.5c (Alamos, Sonora, Mexico), 1979: 2 ♂♂ (dissected), 8 ♀♀ (MZSP); 1 ♂, 3 ♀♀ (AMNH).

Male terminalia. Epandrium (Fig. 7A) microtrichose dorsally and on posterior medioventral area, with about 3 upper and 6 lower setae; ventral lobe expanded posterad (Fig. 7A), partially covering surstylus. Cercus microtrichose, anteromedially fused to epandrium. Surstylus not microtrichose, with about 10 cone-shaped prensisetae, 3 outer and 4 inner setae. Hypandrium (Fig. 7A) shorter than epandrium, anterior margin convex; posterior hypandrial process and dorsal arch absent; gonopod not microtrichose, devoid of seta, connected to paraphysis by membranous tissue. Aedeagus (Fig. 7A–D) dorsodistally bifid and slightly turned dorsad, submedially expanded dorsoventrally; dorsal cleft along most of aedeagus length (Fig. 7B, C); paraphysis not microtrichose, connected to gonopod by membranous tissue, subapically double-walled dorsally, and submedially bearing one setula on dorsal margin (Fig. 7D). Aedeagal apodeme curved ventrad, slightly shorter than aedeagus and fused to it, posterodorsally bifid (Fig. 7C). Ventral rod slightly shorter than paraphysis, dorsoventrally flattened.

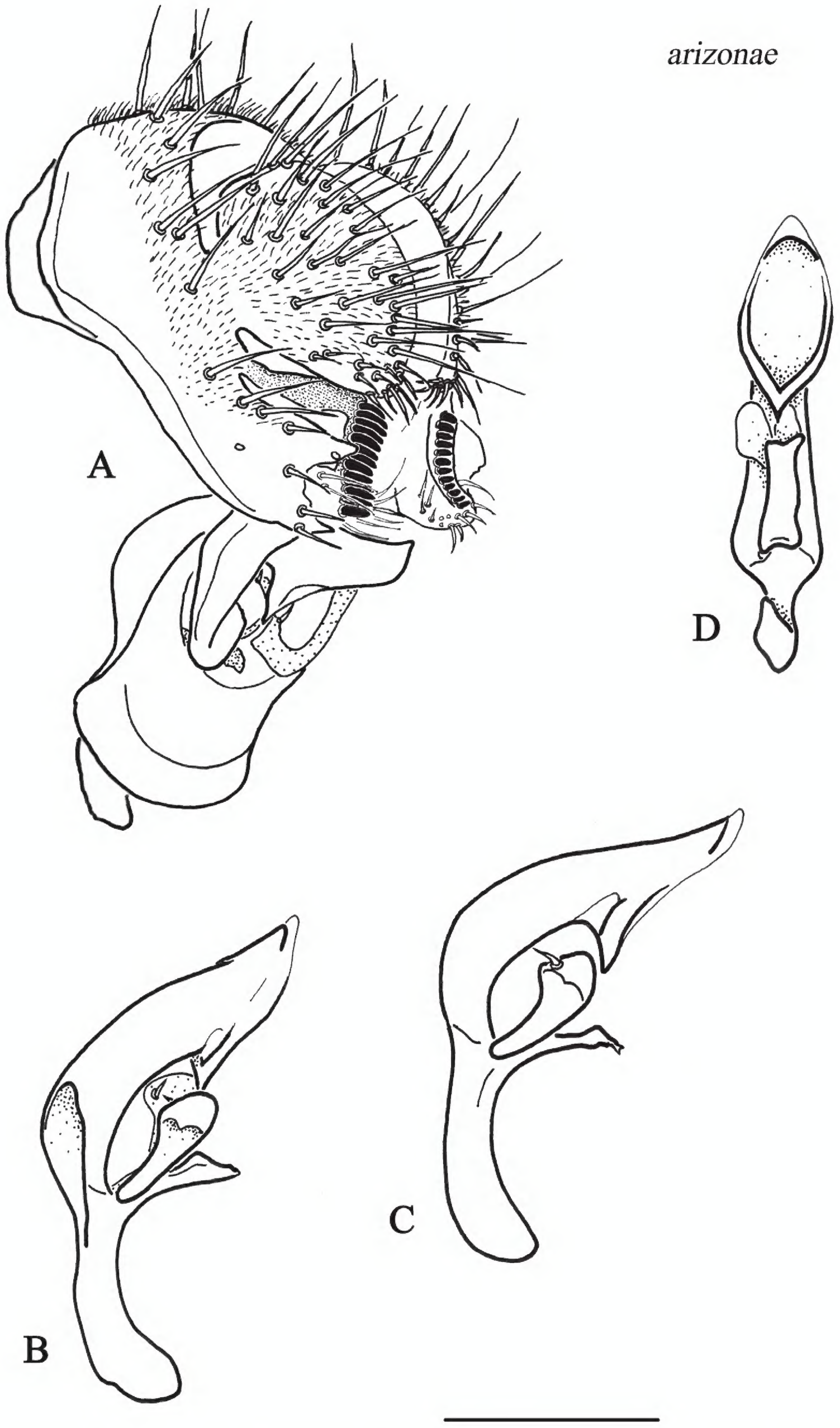

Figure 5. *Drosophila arizonae* Ruiz, Heed & Wasserman, 1990 (*repleta* group, *mulleri* subgroup, *mojavensis* complex). Strain formerly E2.2 at NDSRC (later 15081-1271.4), from Navojoa, Sonora, Mexico, male terminalia (MZSP). **A,** epandrium, cerci, surstyli, hypandrium, aedeagus, paraphyses and aedeagal apodeme, oblique posterior view. **B–D,** aedeagus, paraphyses and aedeagal apodeme, three views. **B,** oblique dorsal. **C,** left lateral. **D,** ventral. Scale bar: 0.1 mm.

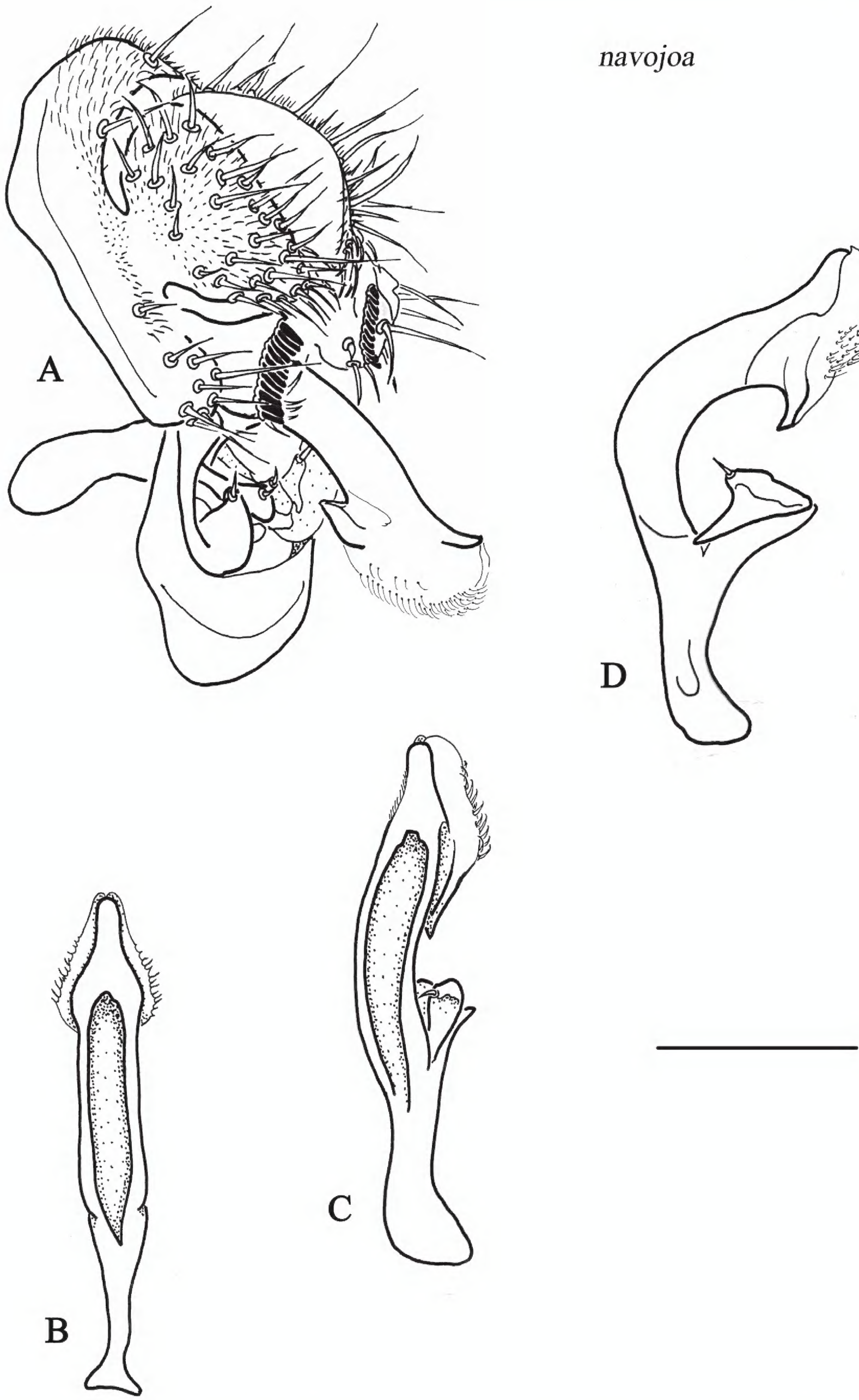

Figure 6. *Drosophila navojoa* Ruiz, Heed & Wasserman, 1990 (*repleta* group, *mulleri* subgroup, *mojavensis* complex). Strain E2.1 at NDSRC, from Navojoa, Sonora, Mexico, male terminalia (MZSP). **A,** epandrium, cerci, surstyli, hypandrium, aedeagus, paraphyses and aedeagal apodeme, oblique posterior view. **B–D,** aedeagus, paraphyses and aedeagal apodeme, three views. **B,** dorsal. **C,** oblique dorsal. **D,** left lateral. Scale bar: 0.1 mm.

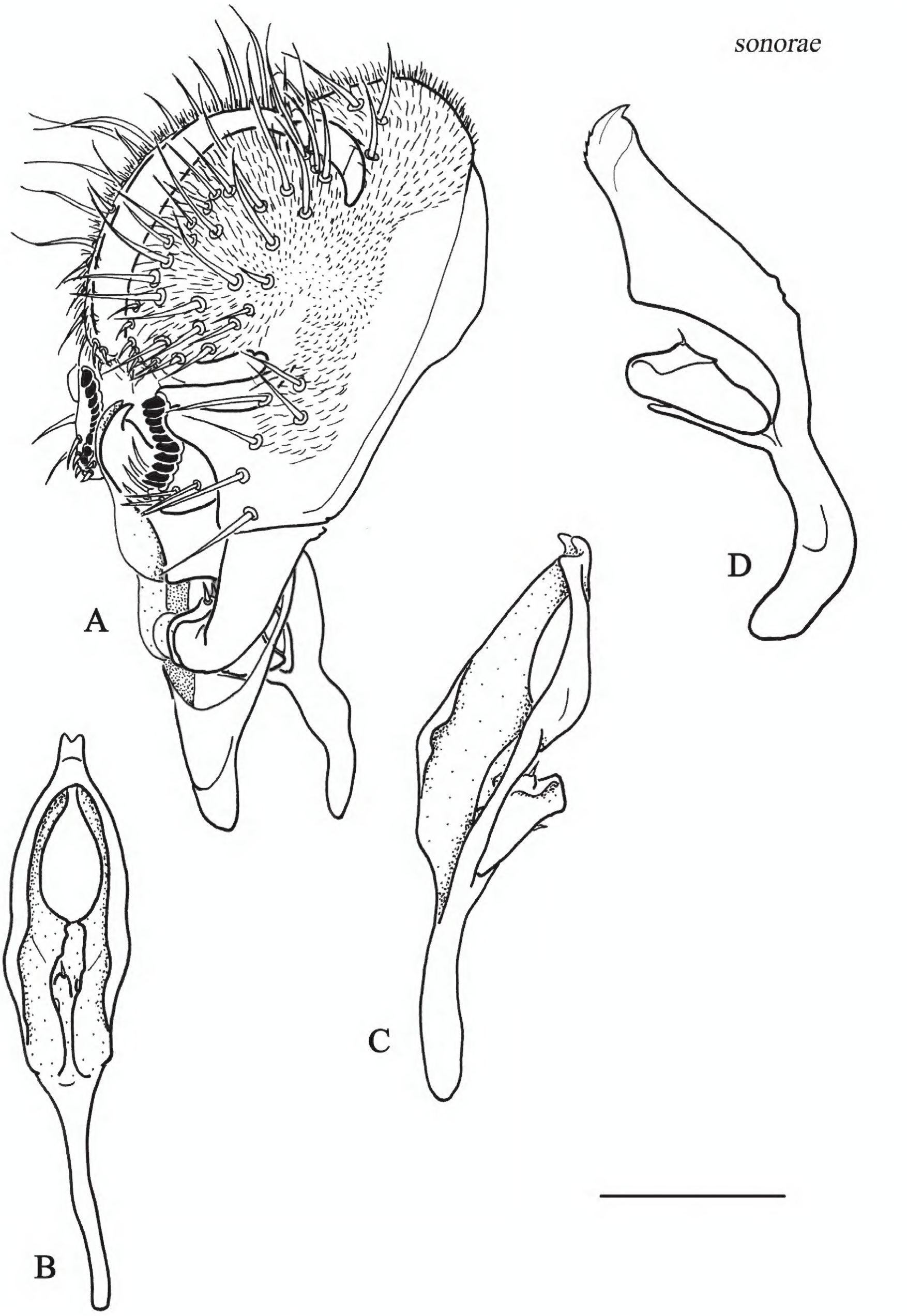

Figure 7. *Drosophila sonorae* Heed & Castrezana, 2008 (*repleta* group, *mulleri* subgroup, *longicornis* complex, *longicornis* cluster). Strain E37.5c at NDSRC, from Alamos, Sonora, Mexico, male terminalia (MZSP). **A,** epandrium, cerci, surstyli, hypandrium, gonopods, aedeagus, paraphyses and aedeagal apodeme, oblique posterior view. **B–D,** aedeagus, paraphyses and aedeagal apodeme, three views. **B,** dorsal. **C,** oblique dorsal. **D,** right lateral. Scale bar: 0.1 mm.

sticta group

Drosophila (*Drosophila*) *sticta* Wheeler

Fig. 8A–J

Drosophila (*Drosophila*) *sticta* Wheeler, 1957: 96.
undetermined/unidentified species of the *Drosophila tripunctata* species group: Vilela 1984: 63, 64.

Male holotype. Double mounted to a point, labelled: "Lancetilla 51.15 / Apr 4, 54 WBHeed / Rep. de Honduras / HOLOTYPE [red label] / Drosophila sticta Wheeler", deposited in NMNH.

Male terminalia. Epandrium (Fig. 8A) dorsodistally microtrichose, with ca. 2 upper and 8 lower setae; ventral lobe posteriorly dorsally membranous, not covering surstylus. Cercus slightly microtrichose on dorsomedial area, linked to epandrium by membranous tissue. Surstylus microtrichose distally on central area, with about 8–9 cone-shaped prensisetae, 4–5 outer and 9–13 inner setae. Decasternum as in Fig. 8B. Hypandrium (Fig. 8C–E) longer than epandrium, anterior margin convex; posterior hypandrial process absent; dorsal arch vestigial, not projected posterad; gonopod not microtrichose, fused to paraphysis, bearing 1–2 long setae on anterior inner margin. Aedeagus (Fig. 8F–J) apically trifid (in dorsal and ventral views, Fig. 8F, J), subapically dilated; the dilatation with a pair of ventral spurs and a dorsal membranous area covered with tiny spines (Fig. 8F–J); dorsal cleft reduced to a small anterior opening (Fig. 8F, G); paraphysis long, conspicuously narrow, slightly widening towards distal end, not microtrichose, fused to gonopod, submedially bearing two setulae on anterior inner surface (Fig. 8E). Aedeagal apodeme 1/3 aedeagus length and fused to it, rod-shaped, posterodorsally bifid (Fig. 8G). Ventral rod vestigial (Fig. 8I, J).

ungrouped

Drosophila (*Drosophila*) *comosa* Wheeler

Fig. 9A–H

Drosophila (*Drosophila*) *comosa* Wheeler, 1968: 432

Male holotype. Double mounted to a point, labelled: "Golfito Costa Rica / WB Heed HL Carson Jun Jul 1959 / HOLOTYPE Drosophila comosa Whlr. [pink label] / Drosophila comosa Wheeler", deposited in NMNH.

Male terminalia. Epandrium (Fig. 9A) distally microtrichose; upper setae absent; ca. 19 lower setae; ventral lobe distally sinuous, partially covering surstylus. Cercus mostly microtrichose, anteromedially fused to epandrium. Surstylus not microtrichose, with about 9 long, sharply pointed prensisetae, 12 outer and 15 inner setae. Decasternum as in Fig. 9B. Hypandrium (Fig. 9C) remarkably developed, twice as long as epandrium, anterior margin convex; posterior hypandrial process and dorsal arch absent; gonopod not microtrichose, devoid of seta, submedially bearing a circular depression adjacent to inner margin; connected to paraphysis by membranous tissue. Aedeagus (Fig. 9D–H) rounded at tip, subdistally expanded ventrad and with a pair of spurs pointed anterad (Fig. 9E–H), dorsally convex at middle and shallowly concave beyond middle; dorsal cleft ca. 1/2 length of aedeagus (Fig. 9D, E); paraphysis conspicuously narrow and curved laterad, not microtrichose, connected to gonopod by membranous tissue, distally double-walled and bearing one setula at the very tip (Fig. 9F). Aedeagal apodeme about 1/3 aedeagus length and fused to it, rod-shaped, posterodorsally bifid (Fig. 9E). Ventral rod vestigial, bifid (Fig. 9G, H).

Discussion

The morphology of the male terminalia harbors highly informative and thus widely used characters for species identification and delineation. The detailed line drawings of the morphology of seven American species depicted here aim at facilitating the identification of these species. In turn, I discuss the implications of these line drawings, the systematics positioning of certain species and give additional comments on the species' distribution range.

Drosophila guayllabambae Rafael & Arcos, 1988

The spot-thoraxed *D. guayllabambae* seems to be a true mountain dweller. This Andean species was described from specimens collected by Gabriela Arcos and Violeta Rafael at 2200 m altitude, 30 km NE of Quito on the right margin of the Guayllabamba River, Guayllabamba, Province of Pichincha, Ecuador. The Guayllabamba River is a tributary of the Esmeraldas drainage system that flows into the Pacific Ocean. The male terminalia of the specimen analyzed in the present paper differ slightly from those depicted in the original description. The differences may be due to both intraspecific variation and different interpretation of the sclerites given by different authors. Thus, it was considered to belong to the same species, which extends the distribution range of *D. guayllabambae* to a slightly lower altitude (ca. 2050 m) of the Andean western slopes of southern Peru (Region or Department of Cuzco). This Peruvian specimen was collected as a byproduct of my incessant and so far unsuccessful quest for a male of the spot-thoraxed *D. peruensis* (see Vilela and Pereira 1985, 1993, Vilela and Bächli 1990, Ratcov and Vilela 2007). The author collected this cited specimen of *D. guayllabambae* on the right margin of the Urubamba River, a tributary of the Amazon drainage system that flows into the Atlantic Ocean. A virtual field trip using Google Earth and Street View software was made in August 2017 to the collection site at kilometer marker 111 of the railroad track. It revealed that the section of the railroad track that once connected Aguas Calientes (km 110) and Machu Picchu (km 112, ca. 1900 m altitude) stations just above the bridge crossing the Urubamba River no longer exists. The 2 kilometers railroad section

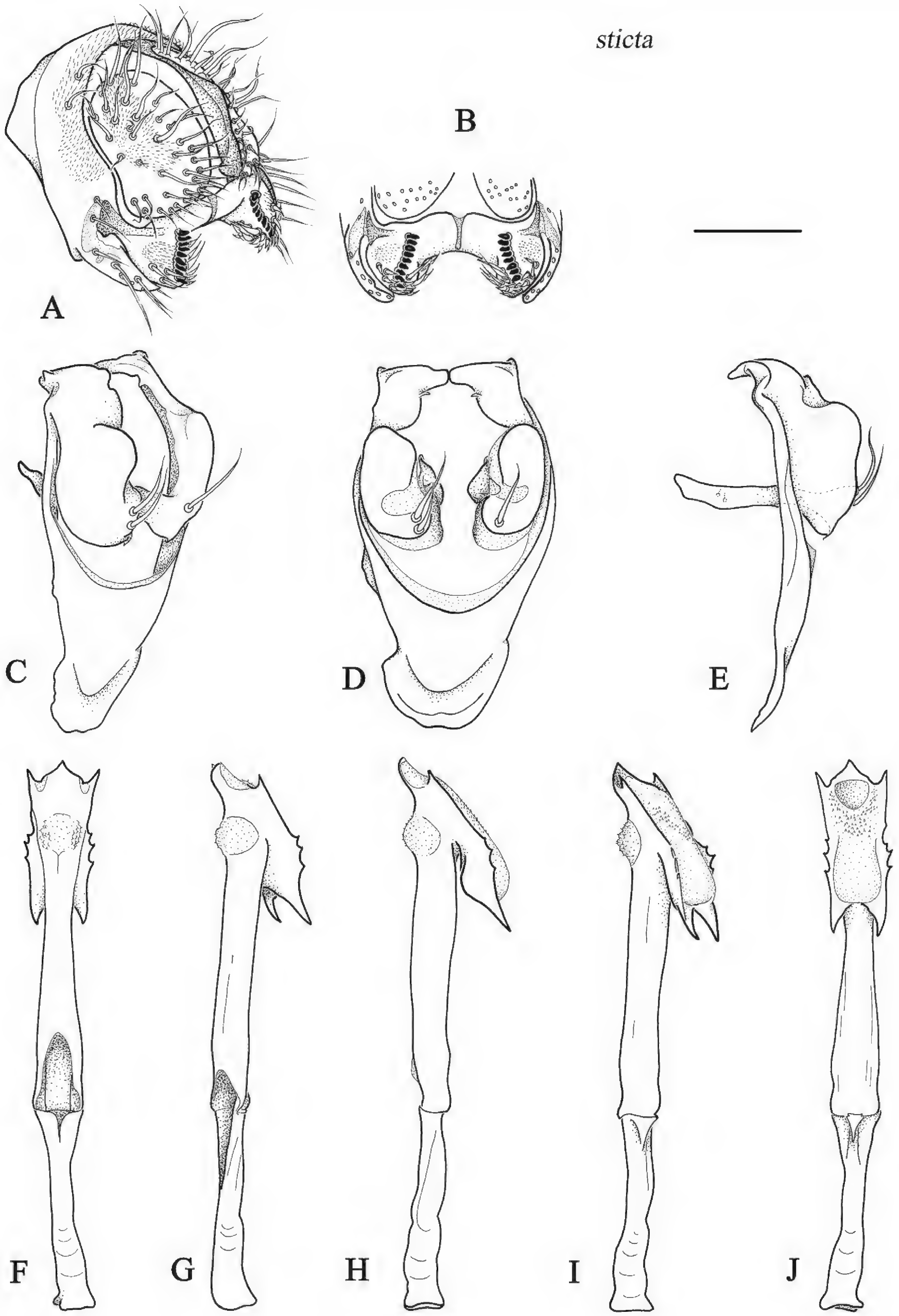

Figure 8. *Drosophila sticta* Wheeler, 1957 (*sticta* group). Holotype from Lancetilla, Honduras, male terminalia (NMNH). **A,** epandrium, cerci, surstyli and decasternum, oblique posterior view. **B,** surstyli and decasternum, posterior view. **C–E**, hypandrium, gonopods+paraphyses, three views. **C**, posterior view. **D,** oblique posterior. **E,** left lateral. **F–J,** aedeagus and aedeagal apodeme, several views from dorsal through ventral. Scale bar: 0.1 mm.

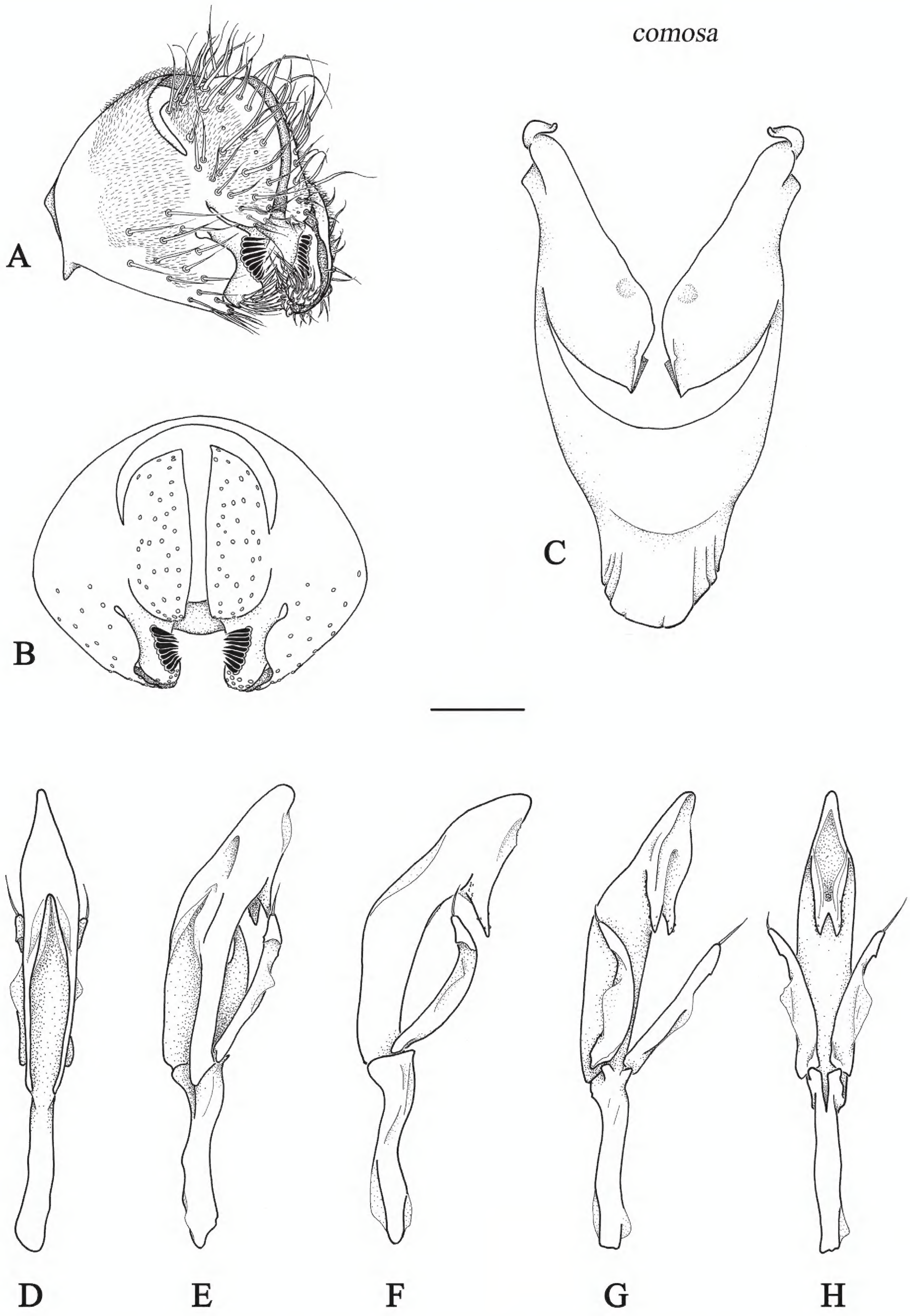

Figure 9. *Drosophila comosa* Wheeler, 1968 (ungrouped). Holotype from Golfito, Costa Rica, male terminalia (NMNH). **A,** epandrium, cerci and surstyli, oblique posterior view. **B,** idem, setae and microtrichiae intentionally omitted, posterior view. **C,** hypandrium and gonopods, posterior view. **D–H,** aedeagus, paraphyses and aedeagal apodeme, several views from dorsal through ventral. Scale bar: 0.1 mm.

has been replaced by an extension of the unpaved Hiram Bingham roadway, currently leading from Machu Picchu pueblo to the Inca city of Machu Picchu. Based on the appearance of the male terminalia sclerites, *Drosophila guayllabambae* is closer to *D. novemaristata* Dobzhansky & Pavan, 1943 (illustrated by Vilela 1983: 36) than to the remaining species belonging to the *hydei* subgroup. The aedeagus of *D. novemaristata* is relatively stouter and shorter (with a relatively longer ventral spur) than that of *D. guayllabambae*.

Drosophila nigrodumosa Wasserman & Fontdevila in Fontdevila et al., 1990

This species is apparently endemic to Venezuela and has a conspicuous surstylus covered with ca. 20 peg-like setae, hence its nickname "bushy tail" used in the NDSRC, Austin. The description of this species was based on specimens sampled from a strain established from flies collected in the Venezuelan Andean mountains at 25 km S of Mérida to San Cristobal, state of Mérida. As it also has been recorded from valleys of lower altitudes of the eastern Cordillera de Mérida, it might not be considered a true mountain species. According to Fontdevila et al. 1990, *D. nigrodumosa* belongs to the *mulleri* cluster of the *mulleri* complex. According to Bächli (2017) it belongs to the *Drosophila mulleri* species complex that also includes *Drosophila aldrichi* Patterson in Patterson & Crow, 1940, *Drosophila huayla* Suyo, Pilares & Vasquez, 1988, *Drosophila mulleri* Sturtevant, 1921, and *Drosophila wheeleri* Patterson & Alexander, 1952.

Drosophila arizonae Ruiz, Heed & Wasserman, 1990

D. arizonae is a Nearctic-Neotropical species occurring from USA (Arizona), Mexico to Guatemala (Brake and Bächli 2008). According to Vilela (1983) it is an extensively-studied species that has been previously cited by many American authors as *Drosophila arizonensis* [not *Drosophila arizonensis* Patterson & Wheeler, 1942; that is a junior synonym of *Drosophila mojavensis* Patterson in Patterson & Crow, 1940]. According to Ruiz et al. (1990), *D. arizonae* belongs to the *Drosophila mojavensis* cluster, together with *Drosophila mojavensis* and *Drosophila navojoa*. The male terminalia line drawings depicted here complement those published by Ruiz et al. (1990).

Drosophila navojoa Ruiz, Heed & Wasserman, 1990

This species is included in the *Drosophila mojavensis* cluster, together with *Drosophila arizonae* and *Drosophila mojavensis* (see Ruiz et al. 1990). The male terminalia line drawings depicted here complement those published by Ruiz et al. (1990).

Drosophila sonorae Heed & Castrezana, 2008

Being placed in the *longicornis* cluster of the *longicornis* complex, this species occurs in the western Mexican states of Sinaloa and Sonora (Heed and Castrezana (2008). The male terminalia line drawings depicted here complement those published by them.

Drosophila sticta Wheeler, 1957

Drosophila sticta occurs from El Salvador to Brazil (Brake and Bächli 2008). This Neotropical species, seldom attracted to fruit-baited traps, was included in a non-diagnosed group of its own by Clayton and Wheeler (1975). Two males belonging to this species emerged from living flowers of *Cestrum intermedium* Sendtn. (Solanaceae) collected by the author in 1982 in the municipality of Santa Isabel, state of São Paulo, Brazil (Vilela 1984). However, at that time, the author was unable to identify those males to species level, and they were just mistakenly cited as "unidentified species of *tripunctata* group" (see also Santos and Vilela 2005). Only after having analyzed and dissected the holotype of *D. sticta* in 1984 the author was able to clarify their identity. Thus, he could also assign to this species a single male specimen collected in 1998 from a banana-baited trap set by Hermes Fonsêca de Medeiros (Medeiros and Klaczko 2004) at Barreiro Rico Farm [currently Bacury Farm], in the municipality of Anhembi, state of São Paulo, Brazil. Later, another single specimen (sex not stated) was collected and identified as *Drosophila sticta* by Garcia et al. (2012) from a banana-baited trap set at the Botanic Garden of Porto Alegre, state of Rio Grande do Sul, Brasil. It is however possible that specimens belonging to this species are present in many collections from different Brazilian states but have not been identified to the species level. The male terminalia illustrations of the holotype of *D. sticta* depicted here (Fig. 8) will complement that of the aedeagus tip in ventral view published in the original description (Wheeler 1957: 91; fig. 13).

Drosophila comosa Wheeler, 1968

In the original description of the *Drosophila comosa*, Wheeler (1968) states that "males of this species have an unusual development of thick hairs on the carina [hence the Latin epithet *comosa*, meaning hairy]" and "females have not been identified as yet". This is a rare and ungrouped species only known from 10 male type specimens (1 holotype and 9 paratypes) collected in Costa Rica on July 4, 1959 by W.B. Heed and H.L. Carson. In the present paper the male terminalia of this species, apparently endemic to Costa Rica, is illustrated for the first time. However, it was of no help in clarifying its relationships with other species, as the general aspect of the sclerites is not similar to any Neotropical species of *Drosophila* known to this author.

Conclusion

The detailed analyses of the male terminalia of selected seven American species of the genus *Drosophila* depicted here reinforce the idea that the knowledge of their component sclerites are essential to reliably tell closely related species apart. Although the terminalia of the Peruvian specimen of *D. guayllabambae* depicted in this paper slightly differ from those illustrated by Rafael and

Arcos (1985) for the Ecuadorian holotype, the two specimens are considered to belong to the same species. The differences may be due to both intraspecific variation and different interpretation of the sclerites given by different authors. This species seems to be a strictly mountainous species of the Ecuadorian and Peruvian Andes, while the remaining six analyzed species occur at variable altitudes of the American continent.

Note

This paper is a tribute to my great master and friend Gerhard Bächli in recognition for his Herculean efforts to create and manage TAXODROS, the indispensable database for anyone working on Taxonomy of Drosophilidae, and for his remarkable devotion to the Mitteilungen der Schweizerischen Entomologischen Gesellschaft as Editor-in-Chief during the past 22 years.

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